Ectomycorrhizas and nutrient transfer in conifer – feather moss ecosystems

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Conifer–feather moss ecosystems dominate large areas of the boreal forest regions of the world, but the interrelations between these two components of the system are poorly understood. Mycorrhizal roots of the trees grow in close association with the mosses. The possibility that nutrients can be transferred from moss shoots to trees through mycorrhizal fungi was investigated using the feather moss *Pleurozium schreberi* and mycorrhizal seedlings of *Pinus contorta*. Shoots of the moss were divided into three categories, viz. green, senescent, and dead, and nutrient contents of aqueous leachates from the segments were measured before and after drying. Significant quantities of nitrogen and phosphorus were released from moss shoots especially after drying. Senescing segments consistently released more N than those that were dead and generally released more than did the green segments. All categories of segments released some protein nitrogen, and drying induced leakage of glucose, fructose, and sucrose. Leachates of entire moss shoots were capable of supporting growth of three mycorrhizal fungi in pure culture. Moss shoots added to chambers containing mycorrhizal plants were colonized by the fungal associates of the plants, particularly intensive growth occurring in the senescent region of the moss shoots. Phosphate (^{32}P) and carbon (^{14}C), previously fed to the moss shoots, was absorbed by mycorrhizal mycelia and transferred over distances of centimetres to infected roots of pine plants and then to their shoots. The significance of these uptake and transfer processes for nutrient cycling in boreal forest ecosystems is discussed.

Key words: leachate, nitrogen, phosphorus, sugars, protein, radioisotope.

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Les écosystèmes à conifères et mousses hypnacées dominent largement de vastes régions des forêts boréales du monde, mais les interrelations entre ces deux constituants du système sont peu connues. Les racines mycorhiziennes des arbres poussent en étroite association avec les mousses. Les auteurs ont étudié la possibilité que les nutriments puissent être transférés des tiges de mousses aux arbres par l'intermédiaire des mycorhizes et ils ont utilisé à cette fin la mousse hypnacée *Pleurozium schreberi* et les pantules mycorhizées du *Pinus contorta*. Les tiges des mousses ont été divisées en trois catégories, *viz.* verte, sénescente, ou morte et les contenus en nutriments des eaux de lessivage de ces segments ont été mesurés avant et après dessication. Des quantités significatives d'azote et de phosphore sont relâchées par les tiges des mousses, surtout après dessication. Les segments sénescents relâchent constamment plus de N que ceux qui étaient morts et habituellement plus que les segments verts. Toutes les catégories de segments relâchent une certaine quantité d'azote protéique et la mort induit une perte de glucose, de fructose et de sucrose. Les lessivats de tiges entières de mousses se sont montrés capables de supporter la croissance de trois champignons ectomycorhiziens en culture pure. Les tiges de mousses placées dans des chambres contenant des plants mycorhizés sont colonisées par les champignons associés aux plants, la croissance étant particulièrement intense dans la région sénescente de la tige de mousse. Le phosphate (^{32}P) et le carbone (^{14}C) préalablement incorporés dans les tiges de mousses sont absorbés par le mycélium mycorhizien et transférés sur des distances de plusieurs centimètres aux racines colonisées des plants de pin et par la suite vers leurs tiges. Les auteurs discutent la signification de ces processus d'absorption et de transfert en relation avec le cyclage des éléments dans la forêt boréale.

Mots clés : lessivats, azote, phosphore, sucres, protéine, radio-isotopes.

[Traduit par la rédaction]

Introduction

In many boreal forest ecosystems the forest floor consists of a continuous carpet of large pleurocarpous feather mosses in the genera *Pleurozium, Hylocomium,* and *Ptilium* (LaRoi and Stringer 1973; Larsen 1980; Lavrenko and Sochava 1956). Such mosses are known to efficiently intercept nutrients contained in precipitation and throughfall (Tamm 1953; Timmer 1970; Oechel and Van Cleve 1986). They thus prevent rapid leaching of nutrients to lower horizons of the soil. In view of its storage capacity, the moss carpet can act as a reservoir in which a large proportion of the potentially available nutrient fund of the ecosystem is sequestered. For this reason feather mosses have been viewed as limiting agents on productivity in spruce – feather moss and pine – feather moss systems by acting as a barrier to nutrient availability for the trees (Oechel and Van Cleve, 1986). However, it has also been recognized that mechanisms may exist for the transfer of nutrients from feather moss carpets to trees.

One possible pathway of nutrient release and transfer is through the decomposer cycle. However, it is known that the mycorrhizal roots of the forest dominants, in conifer – feather moss forests, proliferate most extensively immediately under the moss carpet (Persson 1983; Chapin *et al.* 1987). Extensive mycelial mats associated with these roots are seen under the feather moss carpet, and connections, some of which are likely to be formed by mycorrhizal fungi, can be observed between the senescing moss shoots and these roots. Here the mycorrhizal mycelia are well placed either to intercept leaked mate-

TABLE 1. Nitrogen and phosphorus contents (g/g dry wt.) of leachates from the different categories of moss segments subjected to wet or dry pretreatments and then analysed before or after digestion of the leachate

	Undigested		Digested	
	Wet	Dry	Wet	Dry
Nitrogen				
Green	86.6 ± 12.3	797.0 ± 41.9	443.3 ± 53.9	1596.3 ± 62.0
Senescent	103.1 ± 12.3	809.0 ± 21.0	751.8 ± 33.8	1475.8 ± 136.3
Brown	85.0 ± 10.9	267.2 ± 6.1	690.1 ± 19.8	747.3 ± 46.7
Phosphorus				
Green	0.1 ± 0.01	44.3 ± 1.63	155.1 ± 13.16	191.3 ± 16.55
Senescent	0.7 ± 0.21	52.1 ± 0.45	125.1 ± 19.60	214.7 ± 21.63
Brown	3.6 ± 0.34	63.3 ± 2.24	101.7 ± 19.78	226.5 ± 8.57

NOTE: Values are means of 15 replicate samples ± SE.

rials or even to directly mobilize nutrients contained in the moss carpet, thus short-circuiting the decomposer cycle.

In this paper we determine the nutrient contents and the patterns of nutrient loss from shoots of *Pleurozium schreberi* (Brid.) Mitt, and using microcosms containing mycorrhizal plants with fully developed mycelial systems, we examine the processes of nutrient transfer from individual moss shoots into pine seedlings.

Methods

Mats of *P. schreberi* were collected in August and December 1985 from beneath a *Pinus sylvestris* canopy in the Gwydyr forest, Gwynedd, Wales. These were held in a greenhouse at the Tapton Botanic Garden, University of Sheffield, over a bed of perlite with constant humidification and once daily misting with distilled water. At weekly intervals the mist was supplemented with 1 L of nutrient medium containing 170μg N, 120μg P, and 120μg K. The shoots remained green and healthy throughout the holding period.

Selection of material for analysis

Shoots of *P. schreberi* selected for use were clearly divisible on morphological grounds into two or three increments, each of which has been shown to represent an annual cycle of growth (Oechel and van Cleve 1986). The uppermost segment (*a*) was the entirely green, photosynthetic portion produced in the current year. The middle segment (*b*) consisted of senescing tissue, most of which was 2 years old, and the third segment (*c*) consisted entirely of dead and brown shoot bases, most of which was made up of 3-year-old material. The three segment types were termed (*a*) green, (*b*) senescent, and (*c*) brown.

To determine the potential of each of these categories of segments to supply soluble nutrients to fungi the quantities of the major nutrients nitrogen (N) and phosphorus (P) that could be leached from them were measured. Prior to leaching, one batch of segments of each category was air dried at room temperature for 3 days to simulate a drying episode in the field, whereas the other batch was maintained moist.

Moist and air-dry segments were then immersed in distilled, deionized water for 1 h at room temperature in the ratio 1 g dry wt. moss sample to 40 mL water. The leachate was filtered through Whatman No. 1 filter paper and immediately reduced in volume on a rotary evaporator at 37°C. They were frozen and stored prior to analysis.

Determination of nitrogen, phosphorus, and carbohydrate content of leachates

To mineralize only organic sources of N and P present in the leachates, subsamples were digested in acid prior to nutrient analysis. Five replicated aliquots of all leachate samples were digested in a sulphuric acid and hydrogen peroxide (5:1) mixture at 300°C. The ammonium-N contents of digested and undigested samples were measured using the Nessler procedure (Allen 1974). The phosphorus contents of parallel samples were determined using the ammonium molybdate method (Allen 1974).

TABLE 2. Protein concentrations of leachates of the different categories of undigested moss segments subjected to wet or dry pretreatments

	Wet	Dry
Green	4.27 ± 1.52	5.98 ± 0.12
Senescent	5.38 ± 0.69	6.37 ± 0.39
Brown	5.32 ± 0.19	5.31 ± 0.20

NOTE: Values are means ± SD.

The soluble protein content of a set of undigested samples was determined by the Coumassie-blue procedure. Ethanol-soluble sugar contents of the leachates of undigested samples were determined, after silylation, using standard Pye-Unicam GLC procedures.

Fungal growth experiments

Sterile cultures of *Rhizopogon roseolus* (Corda) T.M.Fr., *Suillus bovinus* (L:Fr.) O. Kuntze, and *Laccaria bicolor* (R. Maire) Orton were grown on modified Melin–Norkran's (MMN) agar. Leachates of dried, whole *P. schreberi* shoots were prepared, as outlined above, such that 40 mL of solution was equivalent to 1 g of shoot dry weight. Four culture solutions were prepared, viz. (*i*) a distilled water (dw) control, (*ii*) distilled water plus dextrose (dw + c; c = dextrose at 10 g L^{-1}), (*iii*) moss leachate (l - c), and (*vi*) leachate plus dextrose (l + c). Each culture solution was passed through a 0.45 μm millipore filter directly into small, sterile Petri dishes with tight-fitting lids. In each dish a 0.75-mm diameter uniform disk of one of the agar cultures was floated on the surface of the liquid. For each fungal species the design was completely randomized as four solution types × five replicates. After 4 weeks at room temperature, the cultures were lifted out onto preweighed filter papers and dried in an oven at 80°C for 12 h. They were weighed following equilibration at room temperature and humidity.

Synthesis of mycorrhizas and establishment of observation chambers

Ectomycorrhizas were first synthesized aseptically in modified plastic Petri dishes of the kind described by Finlay and Read (1986). Each dish was filled with MMN. An aseptically germinated *Pinus contorta* seedling was placed in each dish together with an agar disk from a pure, sterile culture of *S. bovinus*. The dishes were incubated in a propagation chamber for 5 weeks in a growth room exposed to 16-h days at 15°C and 38 W m^{-2} irradiance, with a night temperature of 10°C. At this stage visual observation revealed extensive mycorrhizal formation.

Infected seedlings were then transferred to Plexiglas chambers of two types. The simplest type was flat and comparable with that described by Finlay and Read (1986). it consisted of 20 × 20 cm

TABLE 3. Concentrations of fructose, glucose, and sucrose in leachates from the different categories of undigested moss segments that have been subjected to wet or dry pretreatment

	Wet			Dry		
	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
Green	0	0	0.002	0.992	2.200	2.031
Senescent	0	0	0.001	1.158	2.148	0.875
Brown	0	0	0	0.179	4.435	0.157

TABLE 4. Dry weight yield (mg) of three ectomycorrhizal fungi after growth on media containing leachate of *P. schreberi* and on controlled media for 28 d

	Laccaria bicolor	*Rhizopogon roseolus*	*Suillus bovinus*
Distilled water	0.0140 ± 0.0000	0.0044 ± 0.0008	0.0046 ± 0.0007
Distilled water + glucose	0.0523 ± 0.0005	0.0515 ± 0.0005	0.0527 ± 0.0008
Moss leachate	0.0460 ± 0.0005	0.0485 ± 0.0002	0.0460 ± 0.0009
Moss leachate + glucose	0.0554 ± 0.0016	0.0562 ± 0.0016	0.0604 ± 0.0013

NOTE: Values are means ± SE.

square Plexiglas sheets between which were sandwiched a 1.5-mm layer of nonsterile, milled forest peat. An infected seedling was placed on the surface of the peat of each chamber before the upper sheet was secured in place, and the chambers were incubated in a vertical position under the conditions described above for Petri dish synthesis until an advancing network of mycorrhizal mycelium was visible on the peat surface. At this stage a freshly collected, washed, and towel-dried entire shoot of *P. schreberi* was placed on the peat surface in such a way that the complete length of the shoot was in contact with the peat. Care was taken to arrange the shoot so that all parts were situated at an equal distance from the advancing mycelial front. The growth of mycelium over and around the various portions of the moss shoot was carefully observed and photographed over a period of 4 weeks.

The second type of chamber was designed to enable the photosynthetic part of the moss shoot to be exposed to air. To achieve this objective, two 10 × 10 cm Plexiglas sheets were sealed together at right angles to one another in such a way that one plate, which was to receive the seedling, stood vertically and the other, which was to receive moss shoots, lay horizontally. Peat was spread on each surface, and a further two plates were then applied and clasped in place. For convenience this structure is henceforth termed an L-chamber. An infected seedling was transferred to the upright section of the L-chamber, and as in the case of the flat chamber, the system was incubated until mycelial fans had begun to develop. At this stage moss shoots were placed onto the peat surface in the horizontal part of the L-chamber in such a way that the growing apical portions of the shoots were exposed to the air outside of the chamber. Here only shoots with lengths equivalent to the current year's increment were selected. The chambers were incubated in enclosed, transparent boxes in which saturated vapour pressures were maintained while growth of mycelial fans from the vertical to the horizontal sections took place. Any roots extending in a similar way were cut at the junction of the two sections so that direct pathways from moss to seedling were exclusively through the mycorrhizal mycelium.

Transfer of radioisotope from labelled moss shoot to seedlings in flat chambers

Moist, healthy shoots of *P. schreberi* were labelled with ^{32}P by immersing in a bathing solution of K_2HPO_4 containing 296 MBq of ^{32}P for 1 h. The shoots were surface dried on filter paper and then transfered to a mycorrhizal chamber where they were placed so that they were available for colonization by mycorrhizal mycelia but were lying approximately 10 cm from tree roots when the mycelial fan had extended over and well beyond each moss shoot, a process that took approximately 3 weeks. The upper cover of each chamber was then carefully removed and the peat surface covered in thin acrylic film (Melinex, ICI). Each was autoradiographed by incubating at subzero temperatures in contact with X-ray film for 3 or 4 weeks. *Pleurozium schreberi* shoots were also exposed to $^{14}CO_2$ for 25 h in a growth room. The shoots were similarly placed in observation chambers beyond the mycelial fan. All chambers were maintained in a growth room at 9°C with an 18-h day and an irradiance of 37 W m^{-2}.

Transfer of radioisotope in L-chambers

In this type of chamber, isotope in the form of $^{14}CO_2$ or ^{32}P was fed only to the protruding apical portion of the green moss shoots. For $^{14}CO_2$ feeding the tips were sealed into Plexiglas boxes prior to release of the gas, whereas in the case of ^{32}P they were immersed in a solution of the isotope contained in an open glass vial of 1 mL capacity.

Results

Nitrogen and phosphorus contents of undigested and digested moss segments

Significantly larger concentrations of both N and P were found in the digested than in the undigested extracts of all segments, indicating that the bulk of the leachate was in organic form in the undigested material (Table 1).

The highest concentrations of N, from undigested samples, were obtained in the senescent segments in both the wet and dried treatments. The same was true of the digests from shoots maintained in a moist condition, but the amount of N in the digests of the dried leachates was somewhat higher in the green than in the senescent segments. In all cases, the quantities of N present in the leachates of senescent segments were higher than in those of the brown segments.

Concentrations of P in the leachates of segments of the moist regime were extremely low in all categories (Table 1). Drying led to an increase, the amount of phosphate lost being in the order brown > senescent > green. This order was maintained in leachate digests of the dry treated shoots, though the quantities of P were greatly increased in all segment categories. The digests of the moist treated shoots yielded quantities of P in the reverse order.

Protein concentrations of undigested moss shoots

Concentrations of protein in both wet and dry shoot samples were highest in the senescent segments, but the differences between the categories of segments were small (Table 2).

Sugar concentrations of undigested moss shoots

Negligible quantities of carbohydrates were recovered from the moist shoots. Dry shoots yielded fructose, the highest con-

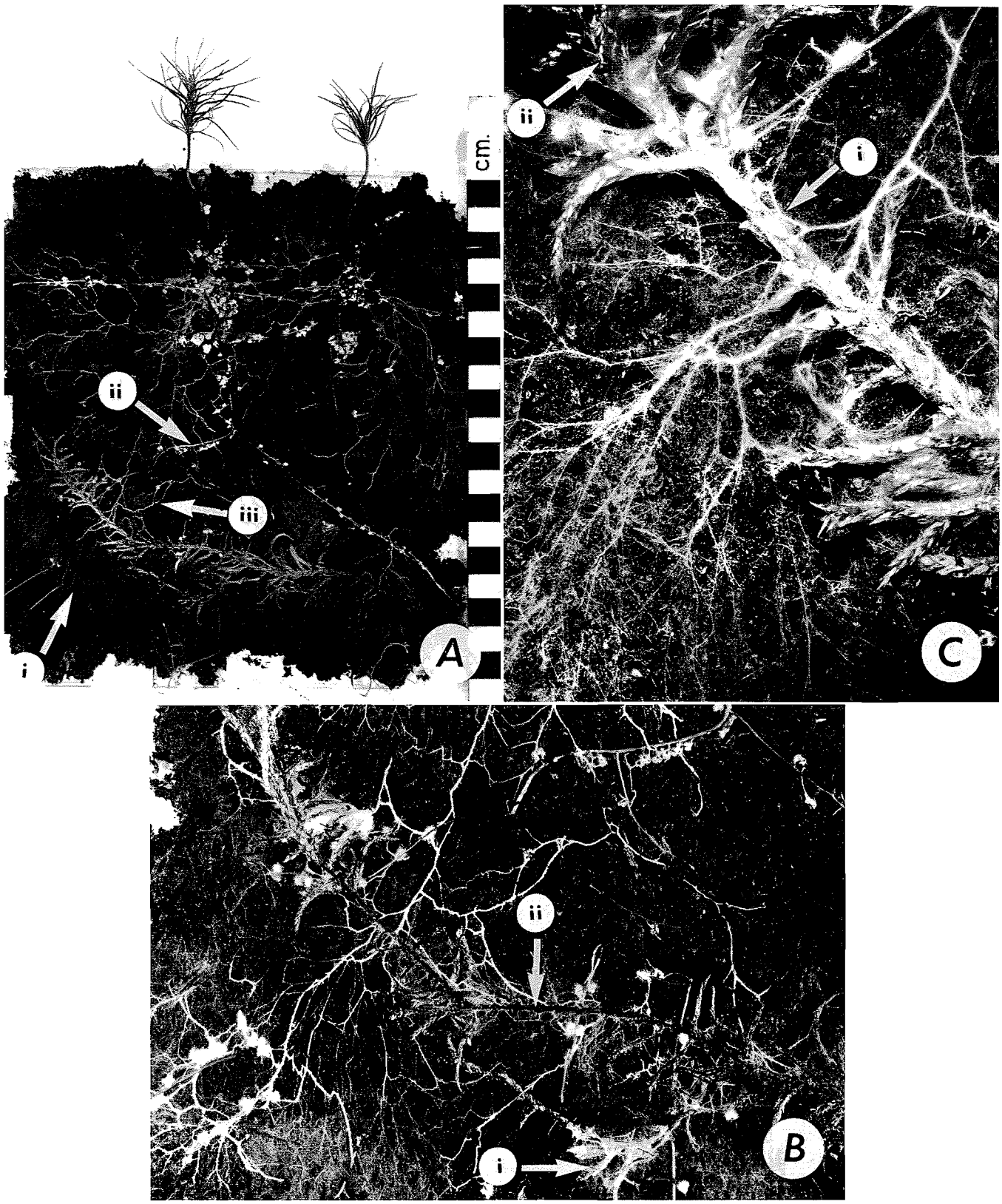

FIG. 1. (A) A mycorrhizal observation chamber, showing two *P. contorta* seedlings infected with *S. bovinus*, 2 weeks after inserting a shoot of *P. schreberi* beyond the advancing front of the mycelium. The mycelium has extended beyond all portions of the moss shoot as an even front (*i*) and is connected to mycorrhizal roots (*ii*) by mycelial strands (*iii*). (B and C) Magnified views of lower (B) and upper (C) portions of the shoot shown in (A) taken after a further 2 weeks growth, showing intensive colonization of senescent portions of the moss shoot (*i* in B and C) and virtual absence of colonization in the green (*ii* in C) and dead (*ii* in B) portions of the shoot.

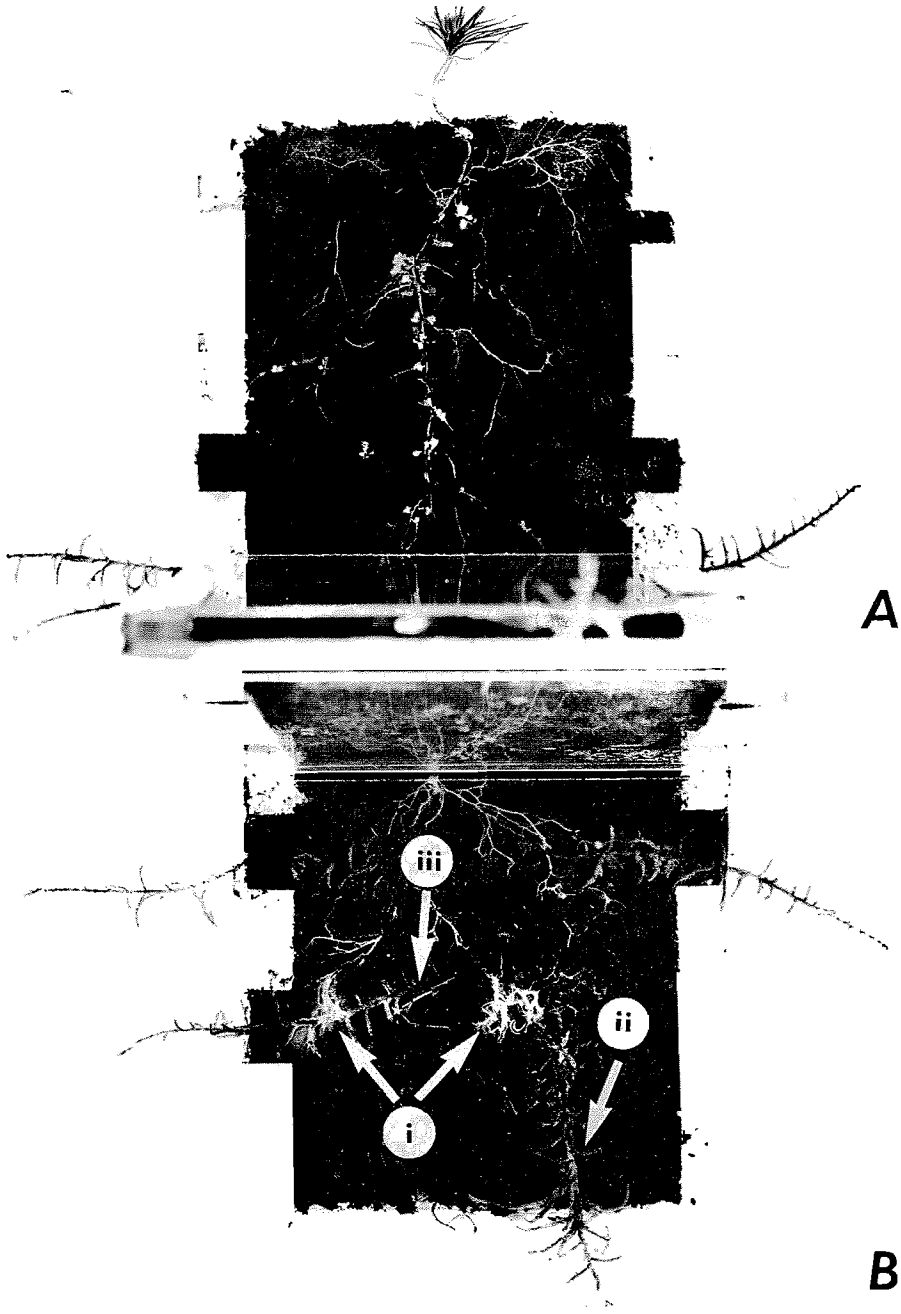

FIG. 2. (A) Surface view of the vertical panel of an L-chamber that holds a seedling of *P. contorta* infected with the mycorrhizal fungus *S. bovinus*. The horizontal panel of the chamber appears end-on, with moss shoots protruding at the sides. (B) Surface view of the horizontal panel of the L-chamber in (A). The shoots of *P. schreberi* lie on the surface of the peat. Strands of *S. bovinus* extend from the base of the vertical panel, beyond which the seedling roots were not allowed to grow, producing strands and distinct sheaths (*i*) around the senescent regions of the moss shoots. Note that the green (*ii*) and dead basal (*iii*) portions of the moss shoots are relatively free of colonization.

centrations of which were found in senescent segments, glucose, which was present in large amounts in brown segments, and sucrose, the concentration of which in leachates from green segments of dried shoots was more than double that in the senescent segments (Table 3).

Fungal growth experiment

The treatment media all produced much greater harvest weights than the distilled water control (Table 4). The pattern of growth response was consistent among the three fungal species. The two sets of treatments with carbon amendment showed the highest yield, and in the case of *S. bovinus* and *R. roseolus*, the leachate plus carbon treatment produced the greatest dry weight. However, leachates by themselves also supported yields comparable with those obtained in the treatment providing carbon alone.

Colonization of moss shoots by mycorrhizal fungi

Daily visual examination of the extending mycorrhizal mycelial system revealed that the mycelial fans reached all parts of the moss shoot at approximately the same time. Growth of the fan subsequently extended beyond the shoot (Fig. 1A). Of greatest interest was the pattern of colonization of the shoot after the mycelial front had passed beyond it. It is clear from

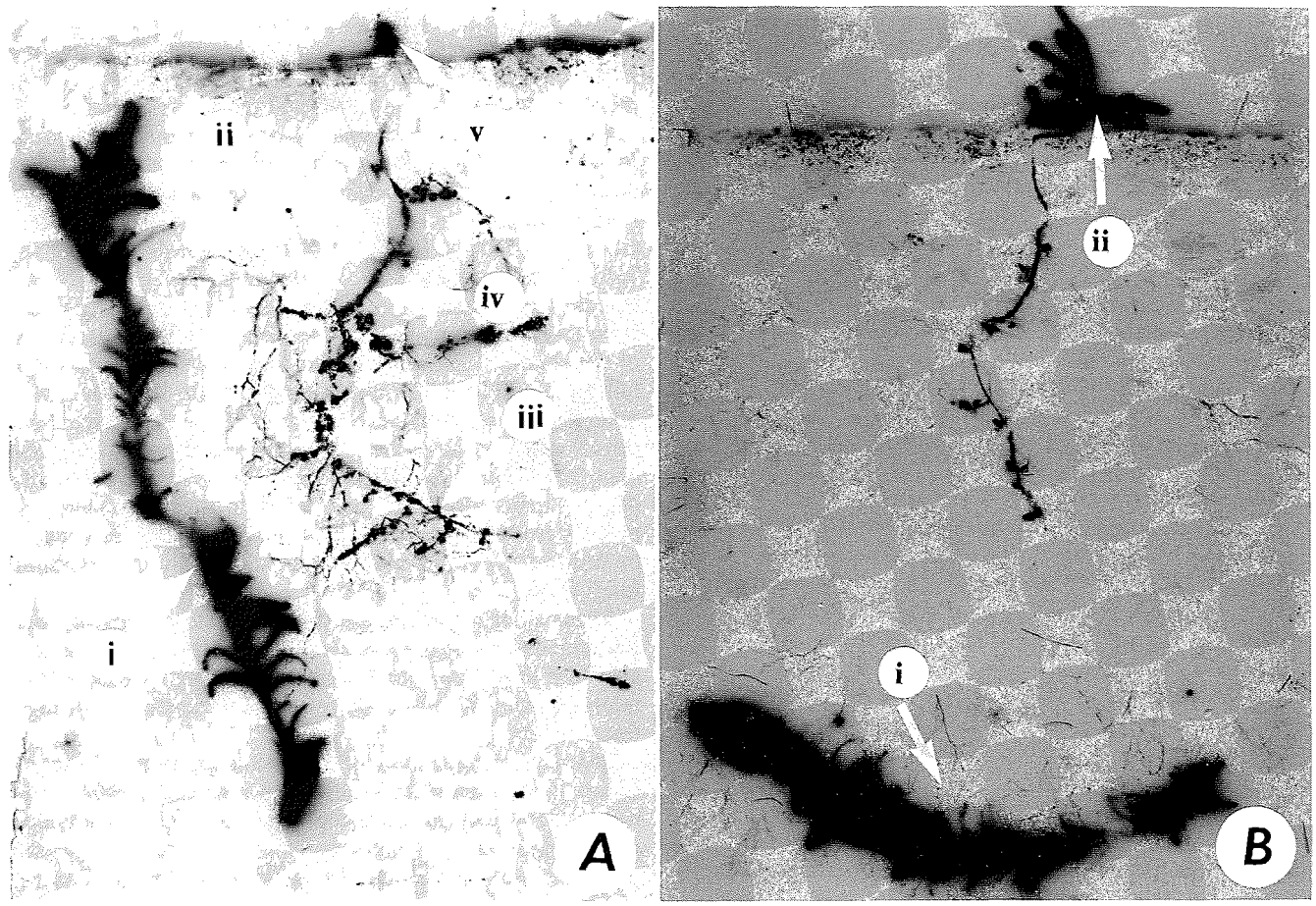

FIG. 3. (A) Autoradiograph of a mycorrhizal observation chamber, as in Fig. 1B, in which a ^{32}P-labelled shoot of *P. schreberi* (*i*) has been placed. Label is clearly visible in the moss shoot, the mycelium (*ii*), the mycorrhizal infection points (*iii*), the root system of the seedling (*iv*), and the base of the stem (*v*). No label is apparent in the peat substrate. The seedling shoot was also heavily labelled (not shown). (B) Autoradiograph of the same type as seen in (A). In this case the detail of label in the fine hyphae (*i*) adjacent to the labelled moss shoot is apparent. Furthermore, the intact shoot of the seedling is seen to be heavily labelled with ^{32}P (*ii*).

Fig. 1B that proliferation of the fungal system is more abundant in some regions of the moss shoot than in others. Thus those parts which retain chlorophyll are lightly colonized by the fungus, whereas in contrast, senescing sections of the shoot situated just below the green portions were enveloped in a dense weft of mycelium (Fig. 1C). The oldest parts of the shoot were relatively little colonized by the fungus (Fig. 1B.)

At the base of the current year's increment of growth the development of mycelium was sufficiently dense to obscure most detail of the moss shoot (Fig. 1C). A structure that was at least superficially comparable with that seen in the sheath of an ectomycorrhiza was produced.

Direct observation of L-chambers

The pattern of colonization of the shorter lengths of moss shoot used in the L-chambers (Fig. 2) was very similar to that observed in the flat chambers described earlier. Intensive exploitation of the moss shoot was restricted to the senescing portions of the current year's shoot where, again, structures superficially reminiscent of sheaths were produced (Fig. 2B).

Transfer of radioisotope through mycelial strands growing from colonized moss shoots

Flat chambers

^{32}P transfer — Autoradiographic analysis of the chambers with ^{32}P show clearly that mycelial connections facilitate the transfer of P from previously labelled shoots to the seedling roots (Fig. 3A) and eventually to the shoots of nearby mycorrhizal plants. The sharply defined image of the moss shoot demonstrates that despite the fact that the labelled shoot had been incubated in contact with the moist peat for at least 3 weeks, very little transport of label had occurred through the peat. Transfer of P from the moss to the tree was therefore entirely dependent upon absorption and translocation through the mycelial system.

^{14}C transfer — As in the case of phosphorus transfer, colonization of the ^{14}C-labelled shoot by the mycelial system provided the potential for movement of the isotope from the shoot into the mycorrhizal strands and thence to the associated plant of *P. contorta* (Fig. 4). Heaviest labelling in the root system of the receiver plant occurs in those parts with a well-developed sheath of mycorrhizal mycelium. The relatively poor definition of the moss shoot in the autoradiograph suggests that labelled material has leaked from it in the course of incubation and that the presence of the fungus has therefore provided a facilitated uptake of material into the peat rather than a direct transfer from the moss shoot.

L-chambers

Autoradiographic analyses of L-chambers after exposure of the growing apices of feather moss shoots to ^{32}P and ^{14}C

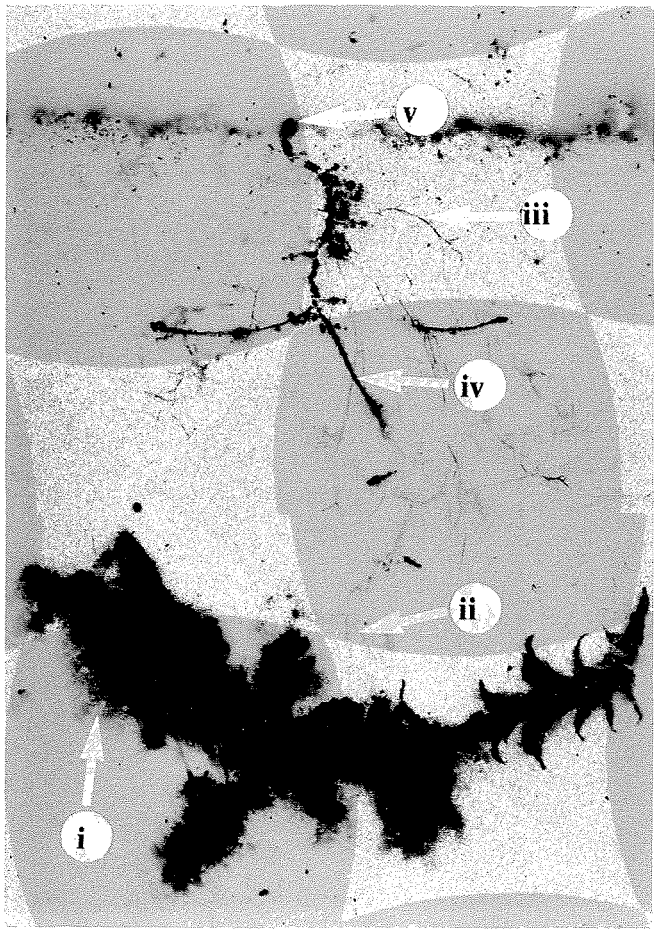

FIG. 4. Autoradiograph of the same type as seen in Fig. 3, but here ^{14}C was the label incorporated into the shoot of *P. schreberi*. Some label was diffused into the surrounding peat substrate (*i*). Note, however, that diffusion of the label does not extend to the seedling roots. Label is clearly visible in fine hyphae (*ii*), mycelial strands (*iii*), infected roots (*iv*), and the stem base of the seedling (*v*). The seedling shoot, which was heavily labelled, was lost during autoradiography.

revealed no evidence whatsoever of transfer of either element beyond the region of the moss shoot that was supplied with the isotope. In the absence of basipetal transfer of labelled material from actively growing regions, export into the mycorrhizal strands is clearly not possible and blank autoradiographs (not shown) are to be expected.

Discussion

The aqueous leachates from *P. schreberi* contain common macronutrients and an energy source in sufficient concentration to support the independent growth of some widespread ectomycorrhizal fungi. It is evident from the increases in leakage observed after drying the moss shoots that release of nutrients in the field might be a sporadic process. Forest mosses are known to encounter wetting and drying periods (Dilks and Proctor 1976), and there is some evidence that the magnitude of leakage is proportional to the length and severity of the drying event. In the boreal system the likelihood is that rewetting of the surface by rain in late summer or fall would be expected to lead to a flush of nutrient release. It is of interest that these events would coincide with a period of intensive physiological activity in the fungal populations, many of which fruit at this time. The surface soil layers of boreal evergreen forests are known to contain high concentrations of mycorrhizal roots (Persson 1983) that are thus ideally placed to absorb nutrients leaked from rewetted and dying moss shoots.

Most of the macronutrients leaking from rewetted shoots of *P. schreberi* appear to be in organic form, the quantities of inorganic N and P being small, as shown earlier by Timmer (1970). Rather it is known that green shoots of the moss contain approximately 1.5–2.5% N by dry weight and that about 75% of this is water soluble. Much of the soluble N in the shoots is in organic form, and some of this is clearly released from living shoot portions on rewetting. In the senescent part of the shoot, at least, the breakdown of cellular compartmentalization will lead to complexing of protein with phenolic and other organic constituents of the moss tissue. The ericoid endophytes certainly have the ability to release protein from such complexes (Leake and Read 1987). Whatever the nature of the organic materials being released from the moss shoot, it is evident from the aseptic fungal growth studies that they can be utilized as carbon and nitrogen sources by the mycorrhizal fungi tested.

These studies confirm not only that ectomycorrhizal mycelial strands colonize particular parts of the feather moss but also that they form direct pathways through which nutrients released from the moss shoots can be transferred to mycorrhizal roots.

Selective colonization of senescent portions of the moss shoots is an interesting feature that is probably related to the pattern of release of nutrients. The green, photosynthetically active region of the feather moss shoot would be expected to retain the bulk of the nutrient that it absorbs from throughfall and precipitation in the living biomass. Although drying can induce leakage from this part of the system, other losses from the living part of the shoot prior to senescence are likely to be small, since in feather moss shoots there is little or no internal conduction of nutrient away from sites of absorption (Skre *et al.* 1983). Major mobilization of nutrients out of a feather moss carpet must, therefore, depend upon the death of tissue and the breakdown of cellular compartmentalization.

There appears to be a gradient of nutrient availability in the shoot of *Pleurozium*, the dead basal parts of the shoot being largely exhausted of materials capable of supporting intensive growth of the fungus. The analyses of sugar content of these segments showed that they contained little or no sugars and relatively small concentrations of P and N. Failure of the fungi to colonize these regions intensively is therefore not surprising. Progressively more nutrient release is observed through the senescent segments in which loss of integrity of the plasmalemma will lead to loss of cellular constituents, particularly after drying cycles. The failure of the fungus to colonize the green parts of the shoot is most probably attributable to the relatively low nutrient efflux rates and the relatively low vapour pressures prevailing around the exposed portions of the moss carpet.

Intensive colonization of that part of the shoot in which cellular integrity is being lost will maximize the chance of direct recycling of those nutrients originally captured by the living shoot portions. Any nutrients leached from apical portions after rewetting will also be intercepted by the weft of fungal material associated with the lower parts of the shoot as they are washed downwards.

It is known that many ectomycorrhizal fungi assimilate simple and complex organic sources of nitrogen. Intensive colo-

nization of senescing parts of the moss shoots would provide these fungi with access to such substrates. The pattern of colonization and transport observed in this study would thus ensure an effective nutrient cycle in which materials contained in the throughfall were absorbed by the moss carpet, subsequently released by the shoots and transferred to the mycorrhizal root.

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